# THE EFFECTS OF PRESCRIBED FIRE ON TREE STRESS AND DISEASE IN OAK DOMINATED FORESTS

By

ALISSA J. FREEMAN

Bachelor of Science in Organismal Biology

University of Kansas

Lawrence, KS

2013

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
July, 2018

THE EFFECTS OF PRESCRIBED FIRE ON TREE STRESS AND DISEASE IN OAK DOMINATED FORESTS

Thesis Approved:

Henry Adams

Thesis Adviser

Janette Steets

Gail Wilson

ACKNOWLEDGEMENTS

I thank Dr. Janette Steets, Dr. Gail Wilson, and, most especially, my advisor Dr. Henry Adams for their invaluable advice, guidance, and encouragement throughout my time at Oklahoma State University. I also thank Dr. Richard Cobb, Dr. Rod Will, and Dr. Stephen Hallgren for their input and guidance throughout my research. Additionally, I thank Jeff Howard at Okmulgee Wildlife Management Area and Jack Waymire at Pushmataha Wildlife Management Area for facilitating my research. Lastly, I thank my partner, David Bowie, and Bill Hammond whom have helped throughout my course of study and research.

Name: ALISSA FREEMAN

Date of Degree: JULY, 2018

Title of Study: THE EFFECTS OF PRESCRIBED FIRE ON TREE STRESS AND DISEASE IN OAK DOMINATED FORESTS

Major Field: BOTANY

Abstract: Incidents of *Quercus* decline have been driven by complicated interactions among factors such as temperature, drought, pathogenic fungi, and tree density, which operate at multiple time scales. In particular, past incidents of elevated tree mortality in response to drought in the highlands of Oklahoma were associated with biotic factors; specifically, the infection of *Quercus* species by canker-causing *Biscogniauxia* fungi. Much research has demonstrated the association between water stress and *Biscogniauxia*, however, little is known about the interactions between forest densification, water stress and fungal infection. I investigated the effects of disturbance regimes on *Biscogniauxia* prevalence at two different sites in Oklahoma—Pushmataha Wildlife Management Area (PWMA) and Okmulgee Wildlife Management Area (OWMA). Stands at PWMA were subjected to 4-year and 1-year fire return intervals, while OWMA stands received 2.5-year and 4.3-year fire return intervals. Utilizing a generalized linear mixed model (GLMM) I found that the incidence of *Biscogniauxia* was highest among units with a fire return interval of 4 years or greater. Additionally, trees exhibiting stress through canopy reduction had greater rates of infection. I measured stable C isotope ratio to investigate treatment effects on tree physiology, however results suggested WUE was highest in units experiencing 4-yr and 1-yr fire return intervals at PWMA, counter to my expectations, while no effect was seen at OWMA. My observations illustrate the effectiveness of disturbance regimes on mitigating pathogenic attack and warrant further investigation to understand the effectiveness of fire regimes as a management strategy.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

**Chapter II**

LIST OF FIGURES

Figures Page

**Chapter II**

# CHAPTER I

# LITERATURE REVIEW

The fungal species *Biscogniauxia* (Xylariales, Xylariaceae)–specifically *B. atropunctata* and *B. mediterranea*— have been associated with elevated tree mortality in response to drought in the oak-hickory forests of Oklahoma, Arkansas, and Missouri (Tainter and Gubler 1973, Bassett et al. 1982, Bassett and Fenn 1984, Jenkins and Pallardy 1995, Masters and Waymire 2012b, Bendixsen et al. 2015). Although not host specific, *B. atropunctata* and *B. mediterranea* are typically associated with *Quercus* species. *Biscogniauxia* spp. have been classified as endophytic in healthy trees and colonizers of the sapwood and bark in hosts stressed by predisposing factors (Ju et al. 1998, Sinclair and Lyon 2005) and can cause necrotic disease. Considered a latent colonizer (Bassett and Fenn 1984), this disease causes tissue death by attacking the phloem and sapwood of oaks, leading to eventual decay, sloughing of the bark, and the appearance of a fungal stroma or canker (Bassett and Fenn 1984, Olson 2013) that may persist on the dead material of hosts for periods of time.

Previous studies have demonstrated that *Biscogniauxia* infection is directly associated with water stressed hosts (Sinclair and Lyon 2005, Vannini et al. 2009).

Bassett and Fenn (1984) simulated water stress on *Quercus* species through girdling, resulting in the appearance of *B. atropunctata* in host tissue. Although *Biscogniauxia* spp. have been found on both living and dead species of *Quercus*, it primarily attacks red oak species (subgenus *Quercus*, section *Lobatae)* (Tainter and Gubler 1973, Bassett et al. 1982, Bassett and Fenn 1984, Haack and Blank 1991a). Tainter and Gubler (1973) found that the decline of moisture content of tissues from 70% to 30% in red oak species resulted in widespread wood decay caused by *B. atropunctata*. Similarly, Vannini and Mugnozza (1991) expressed *B. mediterranea* in water stressed *Quercus cerris* seedlings. Following this study, Vannini et al. (2009) found that *B. mediterranea* infection increased as host water potential decreased in a *Q. cerris* dominated forest. Based on observational studies and field surveys, there is considerable evidence linking increased susceptibility to biotic attack in these forest ecosystems in the face of increased drought frequency and severity. Following the 2013 drought experienced in the southwestern United States, the resulting mortality of white and black oaks were associated with reduced growth during years of high water stress and *Biscogniauxia* infection (Wood et al. 2018).

This water stress can be exacerbated through forest densification, which has occurred across North America due to anthropogenic changes in disturbance regimes (Abrams 1990, Masters 1991, Abrams 1992, Nowacki and Abrams 2008, Burton et al. 2010, DeSantis and Hallgren 2011, Masters and Waymire 2012b). Following the adoption of fire suppression policies since 1930, there have been rippling effects on the composition and structure of ecosystems, as well as a loss of heterogeneity (Brose et al. 2001, Nowacki and Abrams 2008). As a result, many grasslands, prairies, and savannas in the eastern and central US have transitioned to closed-canopy forests with increases in

fire-intolerant woody species replacing the dominant fire-tolerant species through a phenomenon called mesophication (Bragg and Hulbert 1976, Nowacki and Abrams 2008, DeSantis et al. 2010). In particular, oaks require fire for successful regeneration and recruitment, and as such, there has been a reduction of oak dominance in the midstory and sapling layers across the Eastern Deciduous Forest (Brose et al. 2001, Chiang et al. 2008, DeSantis and Hallgren 2011).

By utilizing long-term and broad-scale studies, we can better understand the underlying mechanism of forest compositional shifts brought about through changes in disturbance regimes. DeSantis et al. (2010) resurveyed xeric upland *Quercus* forests located throughout Oklahoma that had been sampled during the 1950's drought (Rice and Penfound 1959), providing unique insight into how the composition and structure had changed in a *Quercus* dominated landscape. Over the 50-year period, total basal area increased by over 94% and total tree density increased by 71%. Likewise, tree density has increased in the highlands of Oklahoma, Arkansas, and Missouri. Historically, these ecosystems were classified as a mosaic of prairie, oak and pine savanna, and oak or pine woodland grasslands (Foti and Glenn 1991, Masters 1991). With the exclusion of fire and less commercial thinning occurring, these ecosystems have transformed to dense homogenous forests composed of predominately oak and pine (Masters 1991). Within this region, the Ouachita mountain landscape has increased in tree density by over 47% (Foti and Glenn 1991, Kreiter 1994, Masters and Waymire 2012b). The increase in density of these *Quercus* dominated landscapes are similar to those observed across the Northern hemisphere (Niklasson et al. 2002, Haavik et al. 2015).

In combination with drought, forest densification has been associated with changes in water availability, often leading to higher rates of tree mortality (Powers et al. 2010, Elkin et al. 2015, Bradford and Bell 2017). A global synthesis of forest mortality events found associations with increased stand density and greater susceptibility to drought induced mortality due to higher rates of competition for water resources (Cobb et al. 2017). Forest management practices such as reducing basal area through mechanical thinning and prescribed burning have been shown to postpone the effects of climate-induced mortality by several decades (Bradford and Bell 2017), and can improve forest health by reducing competition, increasing soil water content as well as hydraulic conductance, resulting in higher photosynthetic rates (Breda et al. 2006, Lechuga et al. 2017). Both experimental (Powers et al. 2010) and simulated studies (Elkin et al. 2015) have investigated the effectiveness of thinning to lessen mortality rates and drought vulnerability, however, few empirical studies have assessed the efficacy of thinning as a long-term solution to meet ecological objectives (Sohn et al. 2013, Elkin et al. 2015, Sohn et al. 2016). Rather, thinning coupled with prescribed fire, or prescribed fire alone, provides greater conditions for oak health restoration (Weatherspoon 1996, Franklin et al. 2003, Albrecht and McCarthy 2006).

Minimal attention has been given to the impact of forest compositional shifts and densification on the prevalence of disease in oak and oak-hickory forests in relation to *Biscogniauxia* species. Secondary fungal pathogens such as these are expected to be positively associated with the predicted increases in drought frequency and severity (Kolb et al. 2016, Wood et al. 2018). As previously mentioned, in the oak-hickory forests, *Biscogniauxia* spp. are often associated with increased drought-stress, which can

be reduced by applying silviculture thinning techniques and prescribed fire. During a 28-year study at the Pushmataha Wildlife Management Area in southeast Oklahoma, Masters and Waymire (2012b) managed experimental units that were initially reduced to presettlement stand densities, then subjected these plots to 4-, 3-, 2-, and 1-year late dormant season fire frequency regimes. During this long-term study, *B. atropunctata* was only found in units experiencing no fire management with highest incidence on *Quercus marilandica* (blackjack oak). Majority of these deaths occurred during periods of below average rainfall and correlated with PDSI values from the preceding 2 years (Masters and Waymire 2012b). However, there were no definitive measurements of tree water stress to implicate the effects of disturbance regimes on the incidence/prevalence of infection and its association with water deficits. Explaining the variable water stress experienced among treatments could provide further supporting evidence for prescribed fire used as a means to improve forest health in these disturbance-associated systems.

There are numerous ways to quantify physiological water stress in trees. A common method for measuring water stress integrated over time is through the use of carbon stable isotopes, the ratio of $^{13}C$ isotopes relative to $^{12}C$ within a leaf—indicating the leaf internal to ambient $CO_2$ concentration. Under optimal conditions, Rubisco has a strong preference towards available $^{12}C$ (Ehleringer et al. 1986). However, during times of stress, stomatal closure leads to a reduction in internal leaf $CO_2$ concentration available for photosynthesis, which has the effect of reducing Rubisco's discrimination against $^{13}CO_2$, leading to an increase in assimilation of $^{13}C$ relative to $^{12}C$ which increases the stable carbon isotope composition ($\delta^{13}C$) of fixed C. $\delta^{13}C$ is indicative of increases in photosynthetic water use efficiency (WUE), the ratio of C assimilated to water transpired,

which can be used to assess drought stress in plants among different environments and species (Ehleringer et al. 1986, Ferrio et al. 2003, Adams and Kolb 2004, Billings et al. 2016). Additionally, $\delta^{13}C$ has been used to specifically evaluate the effect of thinning on tree water stress (McDowell et al. 2006) and provides insight into the mechanistic response of trees to drought (Dawson et al. 2002, Ferrio et al. 2003, Adams and Kolb 2004, Billings et al. 2016). Specifically, increases in WUE inferred from increases in $\delta^{13}C$ has been associated with sensitivity to drought (Ferrio et al. 2003). Although $\delta^{13}C$ has been utilized to answer many broad questions, this measure of drought stress has never been used to assess the impacts of *Biscogniauxia* spp. on tree species in varying environmental conditions.

## Literature Cited


Abrams, M. D. 1990. Adaptations and responses to drought in *Quercus* species of North-America. Tree Physiology **7**:227-238.

Abrams, M. D. 1992. Fire and the development of oak forests- In eastern North-America, oak distribution reflects a variety of ecological paths and disturbance conditions Bioscience **42**:346-353.

Abrams, M. D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Annales Des Sciences Forestieres **53**:487-512.

Adams, H. D., and T. E. Kolb. 2004. Drought responses of conifers in ecotone forests of northern Arizona: tree ring growth and leaf sigma C-13. Oecologia **140**:217-225.

Albrecht, M. A., and B. C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. Forest Ecology and Management **226**:88-103.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere **6**:55.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham,

Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests Forest Ecology and Management **259**:660-684.

Avery, T. E., and H. E. Burkhart. 2015. Forest measurements. Waveland Press.

Bassett, E. N., and P. Fenn. 1984. Latent colonization and pathogenicity of *Hypoxylon atropunctatum* on oaks. Plant Disease **68**:317-319.

Bassett, E. N., P. Fenn, and M. A. Mead. 1982. Drought-related oak mortality and incidence of hypoxylon canker. Arkansas Farm Research **31**:8-8.

Bendixsen, D. P., S. W. Hallgren, and A. E. Frazier. 2015. Stress factors associated with forest decline in xeric oak forests of south-central United States. Forest Ecology and Management **347**:40-48.

Billings, S. A., A. S. Boone, and F. M. Stephen. 2016. Tree-ring δ13C and δ18O, leaf δ13C and wood and leaf N status demonstrate tree growth strategies and predict susceptibility to disturbance. Tree Physiology **36**:576-588.

Bradford, J. B., and D. M. Bell. 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Frontiers in Ecology and the Environment **15**:11-17.

Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie Journal of Range Management **29**:19-24.

Breda, N., R. Huc, A. Granier, and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science **63**:625-644.

Brose, P., T. Schuler, D. Van Lear, and J. Berst. 2001. Bringing fire back - The changing regimes of the Appalachian mixed-oak forests. Journal of Forestry **99**:30-35.

Burton, J. A., S. W. Hallgren, and M. W. Palmer. 2010. Fire frequency affects structure and composition of xeric forests of eastern Oklahoma. Natural Areas Journal **30**:370-379.

Capretti, P., and A. Battisti. 2007. Water stress and insect defoliation promote the colonization of *Quercus cerris* by the fungus *Biscogniauxia mediterranea*. Forest Pathology **37**:129-135.

Carnwath, G. C., and C. R. Nelson. 2016. The effect of competition on responses to drought and interannual climate variability of a dominant conifer tree of western North America. Journal of Ecology **104**:1421-1431.

Chiang, J. M., R. W. McEwan, D. A. Yaussy, and K. J. Brown. 2008. The effects of prescribed fire and silvicultural thinning on the aboveground carbon stocks and net primary production of overstory trees in an oak-hickory ecosystem in southern Ohio. Forest Ecology and Management **255**:1584-1594.

Cobb, R. C., K. X. Ruthrof, D. D. Breshears, F. Lloret, T. Aakala, H. D. Adams, W. R. L. Anderegg, B. E. Ewers, L. Galiano, J. M. Grunzweig, H. Hartmann, C. Y. Huang, T. Klein, N. Kunert, T. Kitzberger, S. M. Landhausser, S. Levick, Y. Preisler, M. L. Suarez, V. Trotsiuk, and M. J. B. Zeppel. 2017. Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. Ecosphere **8**:17.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances **1**:e1400082.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology **37**:451-460.

D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperature forest ecosystems Ecological Applications **23**:1735-1742.

Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics **33**:507-559.

DeSantis, R. D., and S. W. Hallgren. 2011. Prescribed burning frequency affects post oak and blackjack oak regeneration. Southern Journal of Applied Forestry **35**:193-198.

DeSantis, R. D., S. W. Hallgren, T. B. Lynch, J. A. Burton, and M. W. Palmer. 2010. Long-term directional changes in upland *Quercus* forests throughout Oklahoma (vol 21, pg 606, 2010). Journal of Vegetation Science **21**:1001-1001.

Dey, D. C., J. M. Kabrick, and C. J. Schweitzer. 2017. Silviculture to Restore Oak Savannas and Woodlands. Journal of Forestry **115**:202-211.

DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. Weed science:233-242.

Ehleringer, J. R., P. W. Rundel, and K. A. Nagy. 1986. Stable isotopes in physiological ecology and food web research. Trends in Ecology & Evolution **1**:42-45.

Elkin, C., A. Giuggiola, A. Rigling, and H. Bugmann. 2015. Short- and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. Ecological Applications **25**:1083-1098.

Fenn, P., and R. T. Holland. 1984. Changes in wood properties of upland oaks invaded by *Hypoxylon atropunctata* Arkansas Agricultural Experiment Station Report Series:1-9.

Ferrio, J. P., A. Florit, A. Vega, L. Serrano, and J. Voltas. 2003. Delta C-13 and tree-ring width reflect different drought responses in *Quercus ilex* and *Pinus halepensis* Oecologia **137**:512-518.

Field, C. 1986. The photosynthesis-nitrogen relationship in wild plants. On the economy of form and function.

Foti, T. L., and S. M. Glenn. 1991. The Ouachita mountain landscape at the time of settlement. Restoration of old growth forests in the interior Highlands of Arkansas and Oklahoma. Ouachita Nat. For. and Winrock Int. Inst., Morriton, AR:49-66.

Franklin, S. B., P. A. Robertson, and J. S. Fralish. 2003. Prescribed burning effects on upland *Quercus* forest structure and function. Forest Ecology and Management **184**:315-335.

Gleason, K. E., J. B. Bradford, A. Bottero, A. W. D'Amato, S. Fraver, B. J. Palik, M. A. Battaglia, L. Iverson, L. Kenefic, and C. C. Kern. 2017. Competition amplifies drought stress in forests across broad climatic and compositional gradients. Ecosphere **8**.

Haack, R. A., and R. W. Blank. 1991a. Incidence of twolined chestnut borer and *Hypoxylon atropunctata* on dead oaks along an acidic deposition gradient from Arkansas to Ohio. Proceedings, 8th Central Hardwood Forest Conference.

Haack, R. A., and R. W. Blank. 1991b. Incidence of twolined chestnut borer and *Hypoxylon atropunctatum* on dead oaks along an acidic deposition gradient from Arkansas to Ohio.*in* In: McCormick, Larry H.; Gottschalk, Kurt W., eds. Proceedings, 8th Central Hardwood Forest Conference; 1991 March 4-6; University Park, PA. Gen. Tech. Rep. NE-148. Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 373-387.

Haavik, L. J., S. A. Billings, J. M. Guldin, and F. M. Stephen. 2015. Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. Forest Ecology and Management **354**:190-205.

Haavik, L. J., and F. M. Stephen. 2010. Historical dynamics of a native cerambycid, *Enaphalodes rufulus,* in relation to climate in the Ozark and Ouachita Mountains of Arkansas. Ecological entomology **35**:673-683.

Hubbart, J. A., R. Guyette, and R.-M. Muzika. 2016. More than drought: precipitation variance, excessive wetness, pathogens and the future of the western edge of the eastern deciduous forest. Science of the Total Environment **566**:463-467.

Jenkins, M. A., and S. G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **25**:1119-1127.

Ju, Y. M., J. D. Rogers, F. San Martin, and A. Granmo. 1998. The genus *Biscogniauxia*. Mycotaxon **66**:1-98.

Kolb, T. E., C. J. Fettig, M. P. Ayres, B. J. Bentz, J. A. Hicke, R. Mathiasen, J. E. Stewart, and A. S. Weed. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. Forest Ecology and Management **380**:321-334.

Kreiter, S. D. 1994. Dynamics and spatial pattern of a virgin old-growth hardwood pine forest in the Ouachita Mountains, Oklahoma, from 1896 to 1994. Oklahoma State University

Lechuga, V., V. Carraro, B. Vinegla, J. A. Carreira, and J. C. Linares. 2017. Managing drought-sensitive forests under global change. Low competition enhances long-term growth and water uptake in *Abies pinsapo*. Forest Ecology and Management **406**:72-82.

Lloret, F., D. Siscart, and C. Dalmases. 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). Global Change Biology **10**:2092-2099.

Lorimer, C. G. 1985. The role of fire in the perpetuation of oak forests. Challenges in oak management and utilization. . Cooperative Extension Service, University of Wisconsin, Madison, WI, US.

Lutes, D. C., R. E. Keane, J. F. Caratti, H. Carl, N. C. Benson, S. Sutherland, L. J. Gangi, and J. Larry. 2006. FIREMON: Fire effects monitoring and inventory system.*in* F. S. U.S. Department of Agriculture, Rocky Mountain Research Station editor., Fort Collins, CO.

Masters, R. E. 1991. Effects of timber harvest and prescribed fire on wildlife habitat and use in Ouchita Mountains of eastern Oklahoma Oklahoma State University

Masters, R. E., and J. Waymire. 2012a. Developing Management Strategies from Research Pushmataha Forest Habitat Research Area, Oklahoma. Crc Press-Taylor & Francis Group, Boca Raton.

Masters, R. E., and J. R. Waymire. 2012b. Oak savanna restoration: Oak response to fire and thinning through 28 years. In: Dey, Daniel C.; Stambaugh, Michael C.; Clark, Stacy L.; Schweitzer, Callie J., eds. Proceedings of the 4th fire in eastern oak forests conference; 2011 May 17-19; Springfield, MO. Gen. Tech. Rep. NRS-P-102. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 69-91

McDowell, N., H. D. Adams, J. D. Bailey, H. M., and T. E. Kolb. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density chances. Ecological Applications **16**:1164-1182.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology & Evolution **26**:523-532.

Millers, I., D. S. Shriner, and D. Rizzo. 1989. History of hardwood decline in the Eastern United States NE-126, Forest Service.

Niklasson, M., M. Lindbladh, and L. Bjorkman. 2002. A long-term record of *Quercus* decline, logging and fires in a southern Swedish *Fagus-Picea* forest Journal of Vegetation Science **13**:765-774.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and mesophication of forests in the eastern United States Bioscience **58**:123-138.

Olson, J. 2013. *Biscogniauxia* (Hypoxylon) canker and dieback of trees.*in* O. S. University, editor. Oklahoma Cooperative Extenison Service EPP-7620, Stillwater, Oklahoma, USA.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecological Applications **11**:914-927.

Powers, M. D., B. J. Palik, J. B. Bradford, S. Fraver, and C. R. Webster. 2010. Thinning method and intensity influence long-term mortality trends in a red pine forest. Forest Ecology and Management **260**:1138-1148.

Pyne, S. J. 1982. Fire in America: A cultural hisory of wildland and rural fire Princeton University Press, Princeton (NJ).

Rice, E. L., and W. T. Penfound. 1959. The upland forests of Oklahoma Ecology **40**:593-608.

Ryan, K. C. 2000. Effects of fire injury on water relations of ponderosa pine. Pages 58-66 *in* Tall Timbers Fire Ecology Conference Proceedings.

Scheidegger, Y., M. Saurer, M. Bahn, and R. Siegwolf. 2000. Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. Oecologia **125**:350-357.

Sinclair, W. A., and H. H. Lyon. 2005. Diseases of Trees and Shrubs. Cornell University Press.

Smith, A. M., A. F. Talhelm, D. M. Johnson, A. M. Sparks, C. A. Kolden, K. M. Yedinak, K. G. Apostol, W. T. Tinkham, J. T. Abatzoglou, and J. A. Lutz. 2017. Effects of fire radiative energy density dose on *Pinus contorta* and *Larix*

*occidentalis* seedling physiology and mortality. International Journal of Wildland Fire **26**:82-94.

Sohn, J. A., T. Gebhardt, C. Ammer, J. Bauhus, K.-H. Häberle, R. Matyssek, and T. E. Grams. 2013. Mitigation of drought by thinning: short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*). Forest Ecology and Management **308**:188-197.

Sohn, J. A., F. Hartig, M. Kohler, J. Huss, and J. Bauhus. 2016. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. Ecological Applications **26**:2190-2205.

Stahle, D. W., M. D. Therrell, and K. L. Clements. 2003. The Ancient Cross Timbers Consortium for Research, Education, and Conservation: A Proposal from the Tree–Ring Laboratory. University of Arkansas. Retrieved March 15, 2007.

Starkey, D. A., and S. W. Oak. 1989. Site factors and stand conditions associated with oak decline in southern upland hardwood forests. USDA Forest Service general technical report NC North Central Forest Experiment Station.

Sword, M. A., and J. D. Haywood. 1999. Effects of crown scorch on longleaf pine fine roots. Pages 16-18 *in* Proceedings of the tenth biennial southern silvicultural research conference.

Tainter, F., T. Williams, and J. Cody. 1983. Drought as a cause of oak decline and death on the South Carolina coast. Plant Disease **67**:195-197.

Tainter, F. H., and W. D. Gubler. 1973. Natural biological-control of oak wilt in Arkansas Phytopathology **63**:1027-1034.

Thompson, G. E. 1956. Decay of oaks caused by *Hypoxylon atropunctata* Phytopathology **46**:29-29.

Van Arsdel, E. 1972. Some cankers on oaks in Texas. Plant Disease Reporter.

Vannini, A., G. Lucero, N. Anselmi, and A. Vettraino. 2009. Response of endophytic *Biscogniauxia mediterranea* to variation in leaf water potential of *Quercus cerris*. Forest Pathology **39**:8-14.

Vannini, A., and G. S. Mugnozza. 1991. Water-stress- A predisposing factor in the pathogenesis of *Hypoxylon mediterranieum* on *Quercus cerris*. European Journal of Forest Pathology **21**:193-201.

Vannini, A., R. Paganini, and N. Anselmi. 1996. Factors affecting discharge and germination of ascospores of *Hypoxylon mediterraneum* (De Not.) Mill. Forest Pathology **26**:12-24.

Vayreda, J., J. Martinez-Vilalta, M. Gracia, and J. Retana. 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. Global Change Biology **18**:1028-1041.

Wallin, K. F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environmental Entomology **32**:652-661.

Weatherspoon, C. 1996. Fire-silviculture relationships in Sierra forests. University of California, Centers for Water and Wildland Resources

Wood, J. D., B. O. Knapp, R. M. Muzika, M. C. Stambaugh, and L. H. Gu. 2018. The importance of drought-pathogen interactions in driving oak mortality events in the Ozark Border Region. Environmental Research Letters **13**:11.

CHAPTER II

# THE EFFECT OF MANAGEMENT THROUGH PRESCRIBED FIRE ON BISCOGNIAUXIA INFECTION AND TREE STRESS IN OAK DOMINATED FORESTS


## Abstract

Incidents of *Quercus* decline have been driven by complicated interactions among factors such as temperature, drought, pathogenic fungi, and tree density, which operate at multiple time scales. In particular, past incidents of elevated tree mortality in response to drought in the highlands of Oklahoma were associated with biotic factors; specifically, the infection of *Quercus* species by canker-causing *Biscogniauxia* fungi. Much research has demonstrated the association between water stress and *Biscogniauxia*, however, little is known about the interactions between forest densification, water stress and fungal infection. I investigated the effects of disturbance regimes on *Biscogniauxia* prevalence at two different sites in Oklahoma—Pushmataha Wildlife Management Area (PWMA) and Okmulgee Wildlife Management Area (OWMA). Stands at PWMA were subjected to 4-

year and 1-year fire return intervals, while OWMA stands received 2.5-year and 4.3-year fire return intervals. Utilizing a generalized linear mixed model (GLMM) I found that the incidence of *Biscogniauxia* was highest among units with a fire return interval of 4 years or greater. Additionally, trees exhibiting stress through canopy reduction had greater rates of infection. I measured stable C isotope ratio to investigate treatment effects on tree physiology, however results suggested WUE was highest in units experiencing 4-yr and 1-yr fire return intervals at PWMA, counter to my expectations, while no effect was seen at OWMA. My observations illustrate the effectiveness of disturbance regimes on mitigating pathogenic attack and warrant further investigation to understand the effectiveness of fire regimes as a management strategy.

**Keywords**

Prescribed burning; fire suppression; *Biscogniauxia*; oak decline; water use efficiency; oak health; thinning; hypoxylon

**Abbreviations**

OWMA= Okmulgee Wildlife Management Area; PWMA= Pushmataha Wildlife Management Area; FRI= Fire Return Interval; WUE= Water Use Efficiency

## Introduction

Oak decline arising from various causal agents and occurring at multiple time scales has been described worldwide (Millers et al. 1989, Starkey and Oak 1989, Lloret et al. 2004, Vannini et al. 2009, Haavik and Stephen 2010, Bendixsen et al. 2015, Haavik et al. 2015, Cobb et al. 2017, Wood et al. 2018). In the past few decades, there has been a notable increase in pathogenic attack with drought-driven mortality, illuminating the effect of water stress in amplifying fungal disease prevalence across oak-dominated forests of North America; particularly in, Arkansas (Bassett et al. 1982, Bassett and Fenn 1984), Missouri (Tainter et al. 1983, Haack and Blank 1991b, Wood et al. 2018), and Oklahoma (Masters and Waymire 2012b, Bendixsen et al. 2015) in association with *Biscogniauxia* species. Although considered a secondary stress factor, these pathogens can directly lead to tree dieback and death (Thompson 1956, Bassett and Fenn 1984, Sinclair and Lyon 2005, Capretti and Battisti 2007, Olson 2013, Wood et al. 2018). This is cause for concern as oak species compose more than twice the basal area of any other genus in the United States and are typically the dominant species of hardwood forests in the Northern Hemisphere (Millers et al. 1989).

Compounding all of this, anthropogenic changes in disturbance regimes across North America have impacted forests negatively; resulting in fire exclusion and stand densification (Lorimer 1985, Abrams 1992, 1996, Nowacki and Abrams 2008, Burton et al. 2010, DeSantis and Hallgren 2011). With the abandonment of forest management in these ecosystems, forests have also experienced higher rates of competition, increased water stress, and increased mortality rates (Vayreda et al. 2012, Carnwath and Nelson 2016, Gleason et al. 2017, Lechuga et al. 2017). As fire suppression and exclusion has

been adopted, and less commercial thinning has occurred, there have been rippling effects on the composition and structure of ecosystems, as well as loss of oak dominance and heterogeneity of species composition (Nowacki and Abrams 2008, DeSantis et al. 2010). Increased basal area across forest types has been associated with changes in hydrology and water deficits (Powers et al. 2010, Elkin et al. 2015, Bradford and Bell 2017, Gleason et al. 2017). Specifically, soil water availability declines in dense stands which in turn results in stomatal closure and decreasing carbon uptake (McDowell et al. 2011). As drought frequency and intensity increases in an era of higher temperature in dense forests, the atmospheric demand for water of trees also increases, potentially leading to widespread, drought-induced tree mortality (Allen et al. 2010, Allen et al. 2015).

To ameliorate the stress associated with forest densification, thinning treatments that reduce stand density have been applied as a mechanism to amplify resilience and resistance of forest ecosystems and improve resource availability (Powers et al. 2010, D'Amato et al. 2013, Bradford and Bell 2017). In oak dominated landscapes, thinning can open the canopy to these shade-intolerant species, however, oaks are adapted to frequent fires for recruitment and regeneration into the canopy (Abrams 1992, Burton et al. 2010). Prescribed burning is often implemented as a means to maintain reduced basal area, reduce competition from understory vegetation, and mitigate disease. Fire regimes play an important role in promoting plant diversity and woody plant growth and influence compositional shifts towards early successional fire tolerant species adapted to high light exposure (Abrams 1992, Nowacki and Abrams 2008, Burton et al. 2010, DeSantis and Hallgren 2011). Burton et al. (2010) investigated the impact of fire regimes in an oak-dominated forest and found that a fire regime of two or more fires per decade were

necessary to maintain oak dominance and reduce fire-intolerant species, as well as reduce forest density.

Based on observational studies and field surveys, there is considerable evidence linking increased susceptibility to pathogenic attack by *Biscogniauxia* spp. to host water stress (Van Arsdel 1972, Bassett et al. 1982, Bassett and Fenn 1984, Sinclair and Lyon 2005), however, minimal attention has been given to the impact of fire suppression and forest densification on the prevalence of disease. Although *Biscogniauxia* species are considered to be endophytic, they are capable of directly causing tree death and dieback triggered by stress, such as that caused by forest densification. Through the lens of long-term oak management, this study aims to elucidate the relationship between reduced basal area maintained by prescribed fire on the prevalence of *Biscogniauxia* spp. in oak- and oak-pine dominated forests. I utilized field surveys to address whether fire regimes of two fires or more per decade will reduce *Biscogniauxia* prevalence. Explaining the variable water stress experienced among treatments could explain how frequent fire and associated tree density reduction influences tree water stress. One such method of measuring water stress integrated over time is through the use of leaf carbon stable isotopes ($\delta^{13}C$), indicating the internal $CO_2$ concentration. Using leaf $\delta^{13}C$, I compared changes in water use efficiency (WUE) to address whether fire regimes decrease the WUE—resulting in more negative leaf $\delta^{13}C$ —in units burned more frequently. Alternatively, units that have decreased basal area may experience the increases in leaf $\delta^{13}C$ due to increased vapor pressure deficits and high water transpiration. Leaf $\delta^{13}C$ was also used to determine if *Q. marilandica* had higher WUE compared to its co-dominant counterpart, *Q. stellata*, as inferred from leaf $\delta^{13}C$. Here I address the following

questions: (1) Does increased fire frequency—and in turn, reduced basal area— decrease *Biscogniauxia* prevalence? (2) Does reduced competition from the application of prescribed burning result in decreased WUE in oak species? (3) Does *Q. marilandica* have higher WUE than co-dominant *Q. stellata?*

## Methods

*Study Sites*

The study took place at two locations in Oklahoma managed by the Oklahoma Department of Wildlife Conservation under variable strategies, the Okmulgee and Pushmataha Wildlife Management Areas. Located in Okmulgee County in eastern Oklahoma, the Okmulgee Wildlife Management Area (OWMA; Fig. 1) presides on 3700 hectares of land and contains one of the largest areas of old growth forests in the Crosstimbers ecoregion (Stahle et al. 2003). OWMA's canopy is dominated by *Quercus stellata* (post oak), *Quercus marilandica* (blackjack oak), and *Carya texana* (black hickory (Cottam and Curtis 1956).

OWMA has a subtropical climate, receiving an average annual precipitation of 1040 mm, with a mean annual temperature of 16°C. In August, the mean daily high is 34°C while the mean daily low is -2°C in January. The soil at OWMA consists of 13 different types. Of these, Hector-Endshaw soil complex (HtE) covers approximately 75% of the land and is the dominant soil type, composed of stony fine sandy loam that is well drained and non-arable. For my study, I used units that experienced average fire return intervals of 2.5-yr FRI, 4.3-yr FRI, and 30+yr FRI (Table 1a). Units receiving frequent

application of prescribed fire had reduced basal area compared to units that were not frequently burned (Fig 3b). Additionally, *Q. stellata* was found to be the dominant species at all units at OWMA (Fig 3a).

In the south-eastern corner of Oklahoma lies the second study area, the Forest Habitat Research Area (FHRA), located in the Pushmataha Wildlife Management Area (PWMA) which comprises of 7,395 ha within the Kiamichi Mountains in the Ouachita Highland Region. The FHRA is composed of 29.1 hectares of forest dominated by *Quercus stellata* (post oak), *Pinus echinata* (shortleaf pine), *Quercus marilandica* (blackjack oak), and *Carya tomentosa* (mockernut hickory) (Fig 4a). The dominant soil type at the FHRA is Hector-Pottsville soils formed from cherty shales and sandstone (Masters 1991). PWMA has a humid to semi-humid climate, receiving an average annual precipitation of 1244 mm.

Since 1984, the FHRA has experienced consistent and regular management of an initial thinning in selected units in 1984 followed by established fire return intervals. Prior to treatment, the FHRA received fire return intervals greater than 4 years from 1978 to 1984, with basal area ranging from 24-30 $m^2$/ha. In 1984, eight units—including 3-4 replicates per treatment—were implemented at the FHRA to investigate the promotion of oak woodland restoration and these have been maintained to the present day. Five selected units were thinned to pre-settlement densities of approximately 9 $m^2$/ha basal area and either received no prescribed fire or were subjected to 4-, 3-, 2-, and 1-year fire return intervals during dormant season (late February-early April) until present day. Additionally, three units were not mechanically thinned, and were either subjected to 4-, and 1-year fire return intervals or received no prescribed fire. During the last 34 years,

units that were initially thinned but received no fire treatment returned to their initial stand densities and units that were not thinned but were treated with fire at prescribed intervals reached similar stand structure as those that were thinned in 1984 and had the same fire prescriptions (Fig 5). Because mechanical thinning occurred 34-years prior, I was not able to determine the efficacy of thinning apart from burning, and as such, I pooled thinned and unthinned units in groups based on the frequency of fire treatment for statistical analysis. For my study, I used the following units: 34+yr FRI, 4-yr FRI and 1-yr FRI to determine forest health and disease prevalence (Table 1b). Prescribed fire at PWMA effectively reduced basal area in units frequently burned compared to units that received a 34+yr FRI (Fig 4b). All sampling occurred over the summer of 2017.

*Disease Prevalence Survey*

In each unit at both sites (PWMA and OWMA), I established randomly located transects of three replicates per unit using the point-centered quarter plot method (Cottam and Curtis 1956). Each transect began 10 m away from the border of each treatment to reduce edge effect and minimize the impacts from other treatments. For units at PWMA that were 1.2 hectares, one 120 m transect was placed down the center of the unit. If these particular units had a basal area of $9m^2$/ha or less, then all the trees in the unit were measured. For units that were 1.6 hectares or greater (PWMA and OWMA), two 60 m transects were used. Every 20 meters along each transect, I placed a flag vertically to define the center of the point-centered quarter plot for a total of six plots. The area around the point was then divided into quarters, with one-line parallel to the transect, and the other line perpendicular to the transect. In each quarter, the nearest three hardwood trees with a diameter at breast height > 5 cm were measured (Fig 6); identifying species,

diameter at breast height (DBH), presence or absence of oak pathogens, and canopy position. Additionally, I assigned a canopy health rating to assess tree dieback. This included whether the tree had <25% loss of canopy, 25%-50% loss of canopy, >50% loss of canopy, or dead (100% loss of canopy). I assigned all dead stems to the appropriate mortality class and snag decay code according to the FIREMON protocol (Table 2). Species other than *Quercus marilandica* and *Quercus stellata* were categorized as other trees for later analysis. Additionally, at the center of each point, I used a 10-factor wedge prism to quantify tree basal area following standard forestry methods for point sampling (Avery and Burkhart 2015).

*Leaf δ13C and N*

At OWMA I sampled south-facing sun-exposed leaves from the mid-canopy of three healthy *Quercus stellata* trees in dominant canopy positions from the 30+yr FRI unit and units experiencing 4.3-yr and 2.5-yr FRI—including three replicates of each unit. In total, 27 *Q. stellata* trees were sampled at OWMA. Sampling at PWMA occurred in units experiencing 4-yr, 1-yr FRI, and 34+yr FRI. Three individuals in a dominant canopy position of both *Quercus stellata* and *Quercus marilandica* were sampled in each unit with three replicates. 90 trees in total were sampled at PWMA. To minimize intra-seasonal bias, leaves were collected at the end of the growing season in October 2017. Samples were then oven-dried at 70°C and ground to a fine powder with a ball mill. $\delta^{13}C$ and total leaf nitrogen concentration (N) were analyzed at the Stable Isotopes for Biosphere Science Laboratory at Texas A&M University using continuous flow isotope ratio mass spectrometry and an elemental analyzer. Total leaf nitrogen concentration was

used to assess variation of carboxylation capacity which could contribute to any differences seen in leaf $\delta^{13}C$.

*Data Analyses*

I used a Generalized Linear Mixed Model (GLMM) approach to analyze *Biscogniauxia* prevalence among forest management treatments to evaluate what plot-level factors may contribute to disease establishment. Using the Akaike's Information Criterion (AIC) for model selection, I compared the support for different mixed effect binomial models used to predict the presence of *Biscogniauxia* as a function of tree canopy health, tree canopy position, species, diameter, site basal area, and fire return interval. Because site basal area was found to be highly correlated with fire return interval, it was excluded from the analysis. A random effect (replicate) was included in all analyses. For the GLMMM with OWMA data the total number of observations was 486, while PWMA data had 711 total observations. Up to 15 models, including a null model, were constructed for both sites (OWMA and PWMA) with different additive combinations of the independent variables mentioned above as well as their interactive effects (Table 3, Table 4).

To assess what plot-level factors may have influenced tree mortality I constructed seven mixed effect binomial models including a null model, for both OWMA and PWMA, in which survivorship was the response variable and treatment replicates were the random effect (Table 3, Table 4). All analyses were done in R studio 3.3.1 (R Core Team, 2016) using the lme4 package and the function glmer with a binomial distribution and logit link function for mixed effects analyses. Models included the optimization

function bobyqa (Michael J. D. Powell, 2009) and 150000 iterations to deal with model convergence issues. For model selection, I used the bbmle package (Bolker and R Development Core Team, 2011). I chose the set of best models for the GLMMs from OWMA and PWMA using a delta AIC approach. Specifically, I eliminated models from consideration that had a delta AIC score of greater than two.

I compared differences in leaf stable carbon isotope composition ($\delta^{13}C$) among fire regimes using analysis of variance (ANOVA) at both OWMA and PWMA. Total leaf N concentration was used as a proxy for carboxylation capacity to evaluate whether differences carboxylation capacity could account for differences in leaf $\delta^{13}C$ (Field 1986). I used an analysis of variance (ANOVA) to assess for the potential differences in total leaf nitrogen concentration across units at both field sites. Due to the lack of *Quercus marilandica* species at OWMA, I only compared differences in leaf $\delta^{13}C$ between *Q. marilandica* and *Q. stellata* at PWMA, using a Student's t-test. Total leaf N was used to assess differences in carboxylation capacity between species using a Student's t-test at PWMA.

## Results

### *Disease Prevalence and Mortality*

For modeling the presence of *Biscogniauxia* at OWMA, 15 GLMMs were considered with different combinations of main and interaction terms (Table 3). Out of these 15 models, only one had a delta AIC less than two. In this model the presence of *Biscogniauxia* was a function of the additive effects of fire frequency and canopy health

status of the tree (Figure 7). According to this model, the likelihood of *Biscogniauxia* presence was reduced with increasing fire frequency and reduced stress of trees exhibited through canopy health ($P<0.05$, Table 3, Fig 7). *Biscogniauxia* prevalence was highest among dead trees and trees exhibiting a loss of > 50% loss of canopy cover, while *Biscogniauxia* prevalence decreased significantly with reduced loss of canopy cover (Fig 7 b,c,d). An investigative analysis was done to assess the impact of fire frequency alone on the presence of *Biscogniauxia*. I found that management without the additive effect of canopy health was not different among the units at OWMA as seen in Figure 7a.

At PWMA I considered 15 models to model the effect of tree health, tree position in canopy, DBH, site basal area, and fire regimes on *Biscogniauxia* presence at the PWMA (Table 4). I found two models with a delta AIC less than two. Similar to OWMA, my top model with the greatest AIC support was the presence of *Biscogniauxia* as a function of fire return interval and canopy health (Table 4, Figure 8). There was no difference in *Biscogniauxia* presence between dead trees and trees exhibiting a loss of 50% or more canopy cover. Trees exhibiting little to no stress (<50% canopy cover) had significantly reduced *Biscogniauxia* presence (Fig 8b,c,d). Additionally, I assessed the effect of fire frequency alone through an exploratory analysis on *Biscogniauxia* prevalence and found similar results to my best performing model.

To model the potential factors influencing dead trees at OWMA and PWMA, I considered seven models to model the effect of site basal area, fire frequency, and species. I found two models with a delta AIC less than two at PWMA. The best model included the additive effects of fire frequency and species. Units experiencing no fire return intervals had the highest proportion of dead trees (8.6%), while units experiencing

4-yr and 1-yr fire return intervals had 5.4% and 1.7%, respectively. Only units with a 1-yr FRI had a significant difference from the 34+yr FRI units in terms of proportion of dead trees ($P$<0.002, Fig. 8). Interestingly, differences were not found between the proportion of dead *Q. marilandica* and *Q. stellata* which is likely due to the minimal presence of *Q. marilandica* in several of the units ($P$=0.3397). Only 2.7% of the canopy of the 4-yr FRI was composed of *Q. marilandica,* while 26.72% of the canopy in the 1-yr FRI and 12.76% of the canopy in the 34+yr FRI units were composed of *Q. marilandica* (Fig 4). All units had approximately 65% composition of *Q. stellata* (Fig 4). At OWMA, there were no explanatory variables found to explain the percent mortality experienced among the units.

*Leaf δ13C and N*

At OWMA fire regime was not a significant source of variation for leaf δ13C nor leaf N ($P$>0.05, Fig. 9a). At PWMA, fire regime was a significant source of variation for leaf $\delta^{13}C$ ($P$<0.02, Fig 9b). Leaf $\delta^{13}C$ was higher for units receiving 1-year and 4-year fire return intervals compared to the 34+year FRI treatments ($P$<0.02, Fig 9b). *Q. stellata* had lower leaf $\delta^{13}C$ than *Q. marilandica* ($P$ <0.008, Fig. 10). Leaf N did not differ among treatments or between species, indicating that carboxylation capacity did not drive any differences in $\delta^{13}C$ at PWMA.

## Discussion

Fire frequency plays an important role for oak health—encouraging regeneration, reducing competition, and influencing stand density. As frequent fires transitioned to fire exclusion across North America, forest stand densification occurred, leading to forest compositional shifts (Bragg and Hulbert 1976, Nowacki and Abrams 2008, DeSantis et al. 2010). Long-term prescribed fires at PWMA and OWMA were capable of reducing tree basal area and density to stand densities similar to those in the pre-settlement era, with increases in oak dominance (Pyne 1982, Masters and Waymire 2012b). Oaks respond favorably to reduced competition from shade tolerant, fire-intolerant species, under high-light environments, while the inverse is true: oak dominance declines through excessive competition in the absence of fire (Lorimer 1985, Franklin et al. 2003, Lechuga et al. 2017). For two oak-dominated forests in eastern Oklahoma, the greatest predictor of *Biscogniauxia* prevalence was the frequency of prescribed fire and the canopy health status of the tree. At PWMA, units that were burned frequently (FRI ≤ 4 years) had lower basal area, and reduced prevalence of *Biscogniauxia* compared to 34+yr FRI units that had not been burned since 1984. Alternatively, treatments experiencing an average of 4.3-year FRI and 2.5-year FRI at OWMA only had reduced *Biscogniauxia* infection of dead trees compared to the 30+yr FRI unit due to the nearly 100% infection rate of dead *Quercus* species in the 30+yr FRI unit, while both the 4.3-yr and 2.5-yr units had less than 65% infection of dead trees (Fig 7 b,c,d). The additive effect of stress exhibited through the canopy dieback of trees resulted in a higher likelihood of developing *Biscogniauxia* in units experiencing no management application of prescribed fire.

Among the best predictors for *Biscogniauxia* presence in the models for both OWMA and PWMA was tree canopy health, the degree of canopy dieback, which has long been used as an indicator of tree disease (Sinclair and Lyon 2005). Trees exhibiting bare branches and canopy dieback at both forests had a greater prevalence of *Biscogniauxia* canker on boles and/or branches. Trees that were recently dead and trees with canopy loss of 50% or greater had the highest rates of infection.

At PWMA, thinning treatments on their own had little effect on stand density and the prevalence of *Biscogniauxia* infection. Several units were thinned in 1984, however, according to the long-term monitoring of basal area, units that did not receive prescribed fire applications returned to the initial basal area experienced before the application of thinning by 1997 while thinned and unthinned units receiving prescribed fire began to resemble similar basal areas as well (Masters and Waymire 2012b). Due to this prolonged period since thinning, I was unable to properly assess the efficacy of thinning as a management strategy, and I focused primarily on the fire frequency at these units. As found by Weatherspoon (1996), Dey et al. (2017), and Albrecht and McCarthy (2006), this suggests that thinning needs to occur at a regular frequency or may require fire return intervals to maintain ecological benefits. Alternatively, Peterson and Reich (2001) found that long-term applications of fire regimes is sufficient to reduce and maintain stand densities which was supported by the long-term studies conducted at the Forest Habitat Research Area at the PWMA (Masters and Waymire 2012b). Units that were not thinned initially in 1984 and received regular fire return intervals had similar stand characteristics as those that were thinned in 1984, and thus I assessed the impact of fire frequency on health, disregarding the application of thinning in 1984.

Through a combination of active defenses, healthy trees are able to inhibit the growth of hyphae of *Biscogniauxia* (Sinclair and Lyon 2005). Once trees are predisposed to water stress, they are more susceptible to disease. To assess whether reduced stand basal area from prescribed burning accounted for reduced water stress experienced in these units, I inferred water use efficiency (WUE) from the carbon stable isotope composition ($\delta^{13}C$) of leaves. At OWMA I found no differences in leaf $\delta^{13}C$ across fire treatments that reduced basal area. At PWMA, units that experienced 1-yr and 4-yr fire return intervals had a higher (less negative) $\delta^{13}C$ compared to 34+yr FRI units, indicating that these units had higher WUE. This was not consistent with my expectation that WUE would be highest in units with the highest basal areas that had experienced no fire in ~34 years. Notably, differences in $\delta^{13}C$ were relatively small, with the greatest difference of ~0.52 % $\delta^{13}C$ between the 34+yr FRI and 4-yr FRI. This variation in leaf $\delta^{13}C$ was likely not caused by differences in carboxylation capacity, because I found no effect of treatment on leaf N at PWMA.

There are several factors that could have led to this result. Despite reduced basal area in units experiencing 4-yr and 1-yr fire return intervals, it is possible that trees in these units had greater water stress than the 34+yr FRI units. Specifically, the opened canopy in the 1-yr fire return interval has led to increases of forbs and grasses (Masters and Waymire 2012b), resulting in dense understory vegetation which could increase the WUE of the trees. Additionally, low density forests have been associated with increased soil and understory evapotranspiration due to high light exposure and increased vapor pressure deficits (Lechuga et al. 2017). D'Amato et al. (2013) found that although low density forests may experience short term drought resistance, they are more vulnerable

due to the increased water demand by large open-grown trees. Trees in lower density stands tend to allocate more resources to growth, and may have higher hydraulic limitations (Lechuga et al. 2017). Furthermore, fire effects to foliage can alter many aspects of tree physiology; resulting in root damage that could reduce water uptake and increase drought stress (Sword and Haywood 1999), and reduce gas exchange due to damaged foliage and decrease photosynthetic efficiency (Ryan 2000, Wallin et al. 2003, Smith et al. 2017). Recent burns at PWMA experienced several months prior to leaf sampling could have increased WUE. It is also possible that $\delta^{13}C$ were not directly caused by increased water stress in the frequently burned treatments at PWMA. Measurements of $\delta^{13}C$ are used to infer WUE efficiency because more $^{13}C$ is fixed during photosynthesis when internal leaf CO2 concentrations ($C_i$) are low. Stomatal closure from drought stress is often the cause of low Ci, but a low Ci could also be caused by high photosynthetic rates that deplete $CO_2$ faster than it can diffuse from the atmosphere through open stomata (Scheidegger et al. 2000). If oaks in the 1- and 4-yr FRI treatment had higher maximum photosynthetic rates than those in the 34+yr FRI treatment, and stomatal conductance was unaffected by treatment, then differences in $\delta^{13}C$ may not reflect water stress at PWMA. Further investigation is needed to properly assess for variation in water stress experienced by trees among different fire regimes.

Among the two oak species under investigation—*Quercus marilandica* and *Quercus stellata*—leaf $\delta^{13}C$ of *Q. stellata* was more negative, indicating that *Q. marilandica* had greater WUE. This species difference would be consistent with the physiological differences between the white oak group (section *Quercus*, including *Q. stellata*) and red oak group (section Lobate, including *Q. marilandica*). Red oaks tend to

have greater susceptibility to drought, fire injury, and pathogens while white oaks have greater coping mechanisms to deal with cambial injury and fungal infection (Bassett and Fenn 1984, Jenkins and Pallardy 1995, Dey et al. 2017). These species differences were not found to be a significant predictor in the models of *Biscogniauxia* infection, perhaps due to the dominance of *Q. stellata* at the sites I studied. In my surveys, *Q. marilandica* only composed 4.3% of trees at OWMA and 17.8% of trees at PWMA, limiting their ability to affect infection prevalence in the statistical model. Other studies have documented greater decline and association with *Biscogniauxia* spp. in the red oak group (Bassett et al. 1982, Fenn and Holland 1984, Sinclair and Lyon 2005, Bendixsen et al. 2015, Wood et al. 2018), and that *Q. marilandica* was more affected than *Q. stellata* (Rice and Penfound 1959, Bassett et al. 1982).

Although variable water stress inferred from WUE may not have been a factor that influenced disease prevalence, there are several other factors that contribute to the spread and germination of *Biscogniauxia.* Ascospores are considered to have the greatest importance in the dissemination of *Biscogniauxia* spp. (Vannini et al. 1996, Sinclair and Lyon 2005). Following periods of high precipitation or high relative air humidity, ascospores have increased discharge and germination from stromata, and are able to enter wounds and natural openings in otherwise healthy trees (Vannini et al. 1996). The optimal temperature for the germination of ascospores of *Biscogniauxia* species ranges from 30°C to 35°C, with a decline in germination in temperature greater than 40°C (Vannini et al. 1996). During prescribed burns, flames can reach up to one meter and reach temperature of 200°C or greater (DiTomaso et al. 1999), potentially inhibiting

ascospore germination and discharge. Additionally, long-term application of prescribed fire may reduce the spread of ascospores by increasing the distance between host species.

Despite reported drought-induced oak-mortality associated with *Biscogniauxia* (Bassett et al. 1982, Bassett and Fenn 1984, Wood et al. 2018), it is generally not given much consideration as a pathogen capable of inciting high mortality rates or widespread die-off. With climate change, severe droughts are likely to occur with greater frequency and intensity in the Great Plains (Cook et al. 2015), which can be detrimental to forest health, could change that assessment (Allen et al. 2015, Cobb et al. 2017, Wood et al. 2018). Additionally, due to increased energy in the atmosphere with a warming climate, drought is expected to be followed by periods of excessive precipitation (Hubbart et al. 2016), which is favorable for the spread and germination of *Biscogniauxia* spp. (Vannini et al. 1996). With increased water stress, there will likely be increased incidents of pathogen-induced mortality, specifically from *Biscogniauxia* on *Q. marilandica* and *Q. stellata* in the eastern deciduous forests. I propose that the use of frequent fire (FRI $\leq$ 4 years) can effectively reduce the prevalence of *Biscogniauxia* in these fire-adapted ecosystems. To mitigate the anticipated impacts of future climate change, prescribed burning is an invaluable management strategy that promotes drought-tolerant species, reduces competition, maintains low stand density, and reduces disease.

**Acknowledgements**

I thank the Plant Biology, Ecology, and Evolution Department for funding and supporting my research. I'd also like to thank Bill Hammond, Eric Elkins, Justin Dee, Kaitlyn McNiel, and Luke Wilson for field and laboratory assistance.

## Literature Cited

Abrams, M. D. 1992. Fire and the development of oak forests- In eastern North-America, oak distribution reflects a variety of ecological paths and disturbance conditions Bioscience **42**:346-353.

Abrams, M. D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Annales Des Sciences Forestieres **53**:487-512.

Albrecht, M. A., and B. C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. Forest Ecology and Management **226**:88-103.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere **6**:55.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests Forest Ecology and Management **259**:660-684.

Avery, T. E., and H. E. Burkhart. 2015. Forest measurements. Waveland Press.

Bassett, E. N., and P. Fenn. 1984. Latent colonization and pathogenicity of *Hypoxylon atropunctatum* on oaks. Plant Disease **68**:317-319.

Bassett, E. N., P. Fenn, and M. A. Mead. 1982. Drought-related oak mortality and incidence of hypoxylon canker. Arkansas Farm Research **31**:8-8.

Bendixsen, D. P., S. W. Hallgren, and A. E. Frazier. 2015. Stress factors associated with forest decline in xeric oak forests of south-central United States. Forest Ecology and Management **347**:40-48.

Bradford, J. B., and D. M. Bell. 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Frontiers in Ecology and the Environment **15**:11-17.

Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie Journal of Range Management **29**:19-24.

Burton, J. A., S. W. Hallgren, and M. W. Palmer. 2010. Fire frequency affects structure and composition of xeric forests of eastern Oklahoma. Natural Areas Journal **30**:370-379.

Capretti, P., and A. Battisti. 2007. Water stress and insect defoliation promote the colonization of *Quercus cerris* by the fungus *Biscogniauxia mediterranea*. Forest Pathology **37**:129-135.

Carnwath, G. C., and C. R. Nelson. 2016. The effect of competition on responses to drought and interannual climate variability of a dominant conifer tree of western North America. Journal of Ecology **104**:1421-1431.

Cobb, R. C., K. X. Ruthrof, D. D. Breshears, F. Lloret, T. Aakala, H. D. Adams, W. R. L. Anderegg, B. E. Ewers, L. Galiano, J. M. Grunzweig, H. Hartmann, C. Y. Huang, T. Klein, N. Kunert, T. Kitzberger, S. M. Landhausser, S. Levick, Y. Preisler, M. L. Suarez, V. Trotsiuk, and M. J. B. Zeppel. 2017. Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. Ecosphere **8**:17.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances **1**:e1400082.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology **37**:451-460.

D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperature forest ecosystems Ecological Applications **23**:1735-1742.

DeSantis, R. D., and S. W. Hallgren. 2011. Prescribed burning frequency affects post oak and blackjack oak regeneration. Southern Journal of Applied Forestry **35**:193-198.

DeSantis, R. D., S. W. Hallgren, T. B. Lynch, J. A. Burton, and M. W. Palmer. 2010. Long-term directional changes in upland *Quercus* forests throughout Oklahoma (vol 21, pg 606, 2010). Journal of Vegetation Science **21**:1001-1001.

Dey, D. C., J. M. Kabrick, and C. J. Schweitzer. 2017. Silviculture to Restore Oak Savannas and Woodlands. Journal of Forestry **115**:202-211.

DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. Weed science:233-242.

Elkin, C., A. Giuggiola, A. Rigling, and H. Bugmann. 2015. Short- and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. Ecological Applications **25**:1083-1098.

Fenn, P., and R. T. Holland. 1984. Changes in wood properties of upland oaks invaded by *Hypoxylon atropunctata* Arkansas Agricultural Experiment Station Report Series:1-9.

Field, C. 1986. The photosynthesis-nitrogen relationship in wild plants. On the economy of form and function.

Franklin, S. B., P. A. Robertson, and J. S. Fralish. 2003. Prescribed burning effects on upland *Quercus* forest structure and function. Forest Ecology and Management **184**:315-335.

Gleason, K. E., J. B. Bradford, A. Bottero, A. W. D'Amato, S. Fraver, B. J. Palik, M. A. Battaglia, L. Iverson, L. Kenefic, and C. C. Kern. 2017. Competition amplifies drought stress in forests across broad climatic and compositional gradients. Ecosphere **8**.

Haack, R. A., and R. W. Blank. 1991. Incidence of twolined chestnut borer and *Hypoxylon atropunctatum* on dead oaks along an acidic deposition gradient from Arkansas to Ohio.*in* In: McCormick, Larry H.; Gottschalk, Kurt W., eds. Proceedings, 8th Central Hardwood Forest Conference; 1991 March 4-6;

University Park, PA. Gen. Tech. Rep. NE-148. Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 373-387.

Haavik, L. J., S. A. Billings, J. M. Guldin, and F. M. Stephen. 2015. Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. Forest Ecology and Management **354**:190-205.

Haavik, L. J., and F. M. Stephen. 2010. Historical dynamics of a native cerambycid, *Enaphalodes rufulus,* in relation to climate in the Ozark and Ouachita Mountains of Arkansas. Ecological entomology **35**:673-683.

Hubbart, J. A., R. Guyette, and R.-M. Muzika. 2016. More than drought: precipitation variance, excessive wetness, pathogens and the future of the western edge of the eastern deciduous forest. Science of the Total Environment **566**:463-467.

Jenkins, M. A., and S. G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **25**:1119-1127.

Lechuga, V., V. Carraro, B. Vinegla, J. A. Carreira, and J. C. Linares. 2017. Managing drought-sensitive forests under global change. Low competition enhances long-term growth and water uptake in *Abies pinsapo*. Forest Ecology and Management **406**:72-82.

Lloret, F., D. Siscart, and C. Dalmases. 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). Global Change Biology **10**:2092-2099.

Lorimer, C. G. 1985. The role of fire in the perpetuation of oak forests. Challenges in oak management and utilization. . Cooperative Extension Service, University of Wisconsin, Madison, WI, US.

Masters, R. E. 1991. Effects of timber harvest and prescribed fire on wildlife habitat and use in Ouchita Mountains of eastern Oklahoma Oklahoma State University

Masters, R. E., and J. R. Waymire. 2012. Oak savanna restoration: Oak response to fire and thinning through 28 years. In: Dey, Daniel C.; Stambaugh, Michael C.; Clark, Stacy L.; Schweitzer, Callie J., eds. Proceedings of the 4th fire in eastern oak forests conference; 2011 May 17-19; Springfield, MO. Gen. Tech. Rep. NRS-P-102. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 69-91

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology & Evolution **26**:523-532.

Millers, I., D. S. Shriner, and D. Rizzo. 1989. History of hardwood decline in the Eastern United States NE-126, Forest Service.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and mesophication of forests in the eastern United States Bioscience **58**:123-138.

Olson, J. 2013. *Biscogniauxia* (Hypoxylon) canker and dieback of trees.*in* O. S. University, editor. Oklahoma Cooperative Extenison Service EPP-7620, Stillwater, Oklahoma, USA.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecological Applications **11**:914-927.

Powers, M. D., B. J. Palik, J. B. Bradford, S. Fraver, and C. R. Webster. 2010. Thinning method and intensity influence long-term mortality trends in a red pine forest. Forest Ecology and Management **260**:1138-1148.

Pyne, S. J. 1982. Fire in America: A cultural hisory of wildland and rural fire Princeton University Press, Princeton (NJ).

Rice, E. L., and W. T. Penfound. 1959. The upland forests of Oklahoma Ecology **40**:593-608.

Ryan, K. C. 2000. Effects of fire injury on water relations of ponderosa pine. Pages 58-66 *in* Tall Timbers Fire Ecology Conference Proceedings.

Scheidegger, Y., M. Saurer, M. Bahn, and R. Siegwolf. 2000. Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. Oecologia **125**:350-357.

Sinclair, W. A., and H. H. Lyon. 2005. Diseases of Trees and Shrubs. Cornell University Press.

Smith, A. M., A. F. Talhelm, D. M. Johnson, A. M. Sparks, C. A. Kolden, K. M. Yedinak, K. G. Apostol, W. T. Tinkham, J. T. Abatzoglou, and J. A. Lutz. 2017. Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality. International Journal of Wildland Fire **26**:82-94.

Stahle, D. W., M. D. Therrell, and K. L. Clements. 2003. The Ancient Cross Timbers Consortium for Research, Education, and Conservation: A Proposal from the Tree–Ring Laboratory. University of Arkansas. Retrieved March 15, 2007.

Starkey, D. A., and S. W. Oak. 1989. Site factors and stand conditions associated with oak decline in southern upland hardwood forests. USDA Forest Service general technical report NC North Central Forest Experiment Station.

Sword, M. A., and J. D. Haywood. 1999. Effects of crown scorch on longleaf pine fine roots. Pages 16-18 *in* Proceedings of the tenth biennial southern silvicultural research conference.

Tainter, F., T. Williams, and J. Cody. 1983. Drought as a cause of oak decline and death on the South Carolina coast. Plant Disease **67**:195-197.

Thompson, G. E. 1956. Decay of oaks caused by *Hypoxylon atropunctata* Phytopathology **46**:29-29.

Van Arsdel, E. 1972. Some cankers on oaks in Texas. Plant Disease Reporter.

Vannini, A., G. Lucero, N. Anselmi, and A. Vettraino. 2009. Response of endophytic *Biscogniauxia mediterranea* to variation in leaf water potential of *Quercus cerris*. Forest Pathology **39**:8-14.

Vannini, A., R. Paganini, and N. Anselmi. 1996. Factors affecting discharge and germination of ascospores of *Hypoxylon mediterraneum* (De Not.) Mill. Forest Pathology **26**:12-24.

Vayreda, J., J. Martinez-Vilalta, M. Gracia, and J. Retana. 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. Global Change Biology **18**:1028-1041.

Wallin, K. F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environmental Entomology **32**:652-661.

Weatherspoon, C. 1996. Fire-silviculture relationships in Sierra forests. University of California, Centers for Water and Wildland Resources

Wood, J. D., B. O. Knapp, R. M. Muzika, M. C. Stambaugh, and L. H. Gu. 2018. The importance of drought-pathogen interactions in driving oak mortality events in the Ozark Border Region. Environmental Research Letters **13**:11.

## Tables

**Table 1.** Fire return intervals for sites at **a)** OWMA and **b)** PWMA

**a)**

| Fire Return Interval | Description | N |
|---|---|---|
| **30+yr** | Control, no burning | 6 |
| **4.3-yr** | Late-winter prescribed burn, average of 4.3-year interval | 3 |
| **2.5-yr** | Late-winter prescribed burn, average of 2.5-year interval | 6 |

**b)**

| Fire Return Interval | Description | N |
|---|---|---|
| **34+yr** | Control, no burning | 6 |
| **4-yr** | Late-winter prescribed burn, 4-year interval | 3 |
| **1-yr** | Late-winter prescribed burn, 1-year interval | 6 |

**Table 2**. Snag codes and descriptions from the FIREMON protocol (Lutes et al. 2006)

| Snag code | Limbs | Top of bole | Bark | Sapwood | Other |
|---|---|---|---|---|---|
| **1** | All present | Pointed | 100% remains | Intact | Height intact |
| **2** | Few, limbs | May be broken | Some loss, variable | Some decay | Some loss in height |
| **3** | Limb stubs only | Usually broken | Start of sloughing | Some sloughing | Broken top |
| **4** | Few or no limb stubs | Always broken some rot | 50% or more loss of bark | Sloughing evident | Loss in height always |
| **5** | No limbs or limb stubs | Broken and usually rotten | 20% bark remaining | Sapwood gone | Decreasing height with rot |

**Table 3.** GLMM summaries for OWMA

| OWMA Models | AIC | ΔAIC | d.f. | Weight |
|---|---|---|---|---|
| *Biscogniauxia* = FRI + Canopy Dieback | 262.9 | 0.0 | 8 | 0.8001 |
| *Biscogniauxia* = FRI + Canopy Dieback + Species | 265.7 | 2.8 | 7 | 0.1964 |
| *Biscogniauxia* = Species + Canopy Dieback | 274.6 | 11.7 | 6 | 0.0023 |
| *Biscogniauxia* = Species * Canopy Dieback | 276.8 | 13.9 | 8 | <0.001 |
| *Biscogniauxia* = Canopy Dieback | 277.8 | 14.9 | 5 | <0.001 |
| *Biscogniauxia* = FRI + Canopy Position | 288.1 | 25.1 | 10 | <0.001 |
| *Biscogniauxia* = Canopy Position | 300.7 | 37.8 | 8 | <0.001 |
| *Biscogniauxia* = FRI + Species * DBH | 518.7 | 255.7 | 7 | <0.001 |
| *Biscogniauxia* = FRI + DBH | 521.9 | 259.0 | 5 | <0.001 |
| *Biscogniauxia* = DBH | 524.2 | 261.3 | 3 | <0.001 |
| *Biscogniauxia* = FRI * Species | 537.6 | 274.7 | 6 | <0.001 |
| *Biscogniauxia* = FRI | 537.8 | 274.9 | 4 | <0.001 |
| *Biscogniauxia* = FRI + Species | 539.4 | 276.4 | 5 | <0.001 |
| *Biscogniauxia* = Null | 539.8 | 276.9 | 2 | <0.001 |
| *Biscogniauxia* = Species | 541.6 | 278.7 | 3 | <0.001 |

**Table 4.** GLMM summaries for PWMA

| PWMA Models | AIC | ΔAIC | d.f. | Weight |
|---|---|---|---|---|
| *Biscogniauxia* = FRI + Canopy Dieback | 220.7 | 0 | 7 | 0.6781 |
| *Biscogniauxia* = FRI + Canopy Dieback + Species | 222.5 | 1.7 | 8 | 0.2871 |
| *Biscogniauxia* = FRI + Canopy Dieback * Species | 227.0 | 6.3 | 11 | 0.0297 |
| *Biscogniauxia* = Canopy Dieback | 231.2 | 10.5 | 5 | 0.0036 |
| *Biscogniauxia* = Species + Canopy Dieback | 233.1 | 12.4 | 6 | 0.0014 |
| *Biscogniauxia* = Species * Canopy Dieback | 237.1 | 16.4 | 9 | <0.001 |
| *Biscogniauxia* = FRI + Canopy Position | 251.2 | 30.5 | 8 | <0.001 |
| *Biscogniauxia* = FRI * Species | 306.8 | 86.1 | 7 | <0.001 |
| *Biscogniauxia* = FRI + Species | 307.9 | 87.1 | 5 | <0.001 |
| *Biscogniauxia* = FRI + Species * DBH | 308.8 | 88.1 | 7 | <0.001 |
| *Biscogniauxia* = FRI | 309.9 | 89.2 | 4 | <0.001 |
| *Biscogniauxia* = FRI + DBH | 311.7 | 90.9 | 5 | <0.001 |
| *Biscogniauxia* = Species | 323.6 | 102.9 | 3 | <0.001 |
| *Biscogniauxia* = Null | 325.6 | 104.8 | 2 | <0.001 |
| *Biscogniauxia* = DBH | 327.6 | 106.8 | 3 | <0.001 |

## Figures

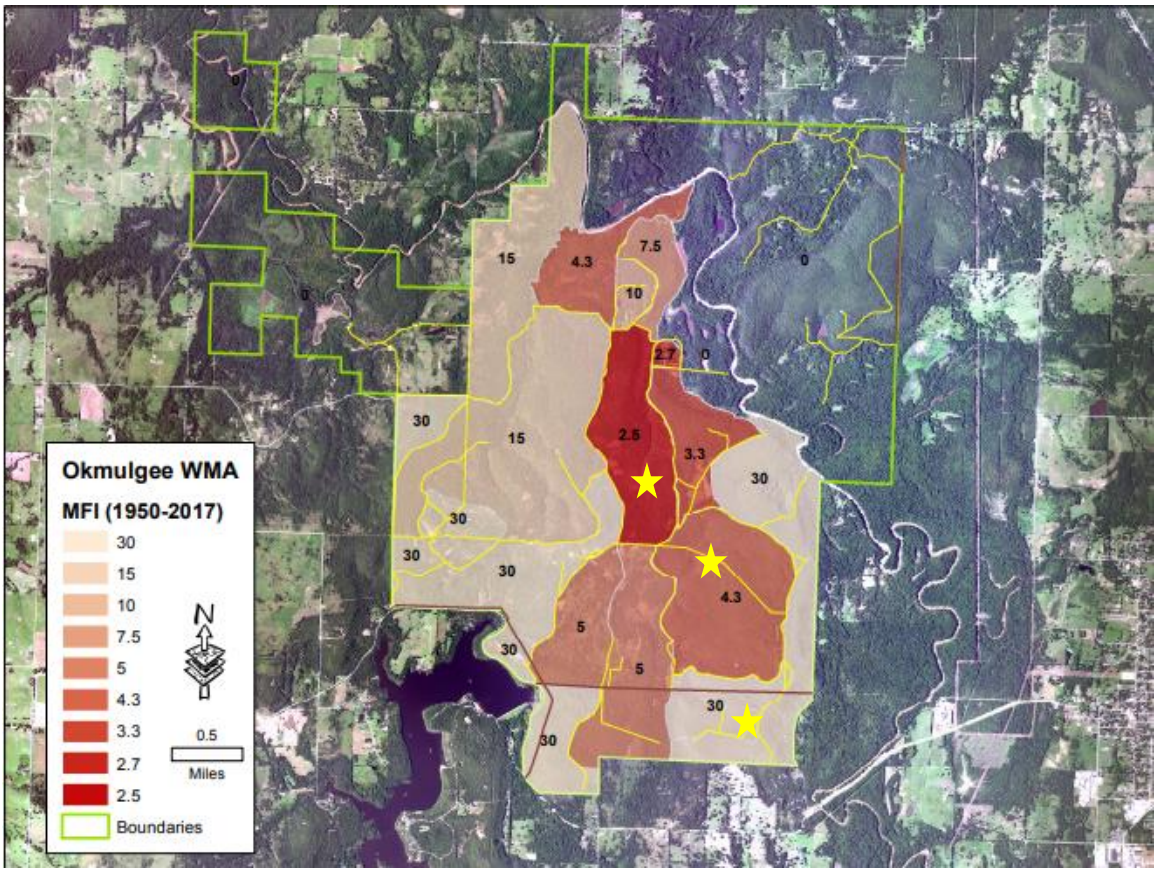


**Fig 1.** Map of OWMA fire regimes (Howard, unpublished) with the mean fire interval (MFI) from 1950-2017 represented by varying colors. Starred units represent the units selected for the study (2.5-yr MFI, 4.3-yr MFI, and 30+yr MFI).


**Fig 2.** Map of the Forest Habitat Research Area at PWMA (Masters and Waymire 2012a). Selected units highlighted in red signify the fire return interval (FRI) of treatments used for the study.

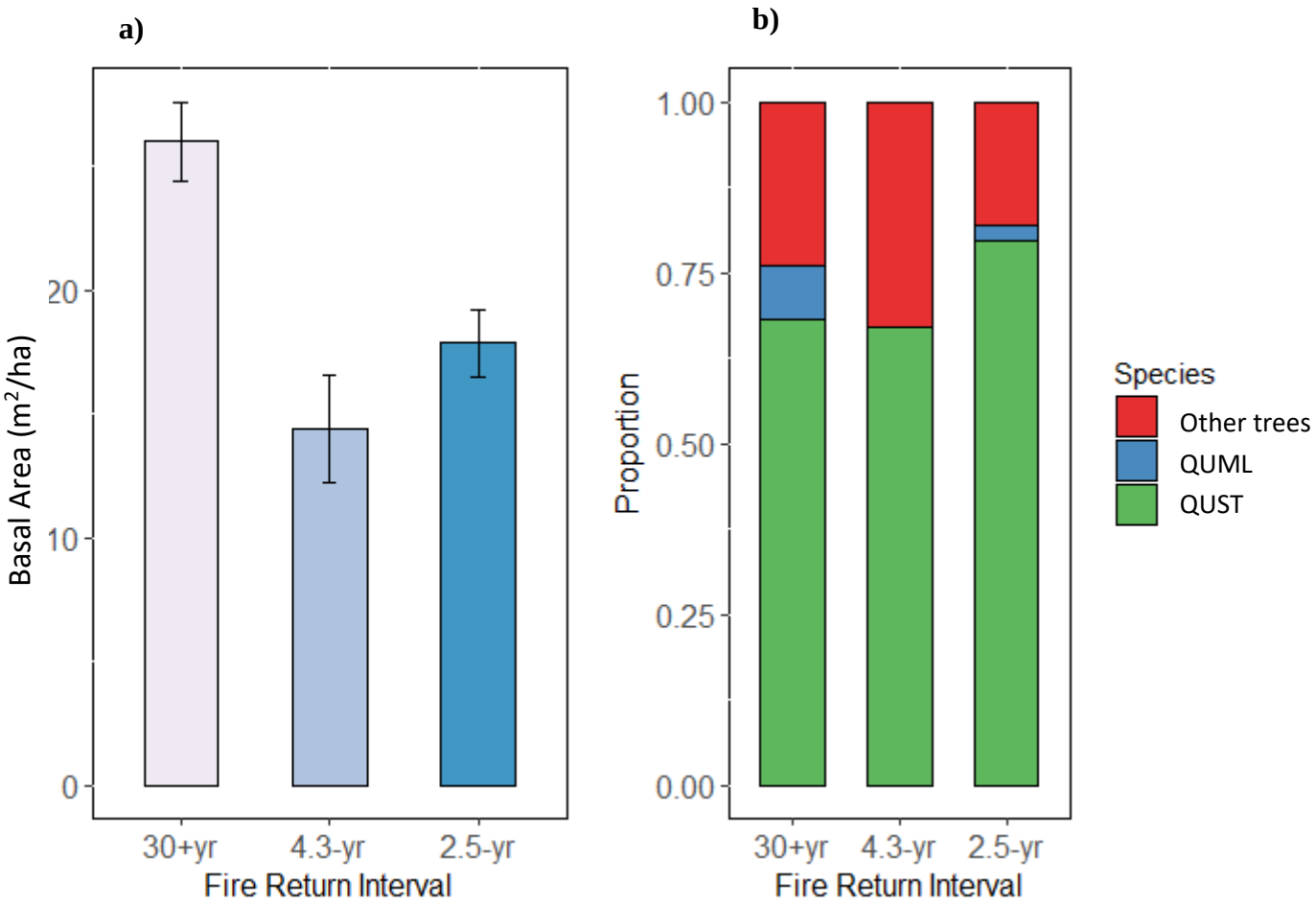


**Figure 3. a)** Mean basal area (BA) of selected units at OWMA and **b)** the species composition of selected units at OWMA including *Quercus marilandica* (QUML), *Quercus stellata* (QUST), and other trees, which included *Carya texana*, *Carya tomentosa*, *Ulmus alata*, and *Ulmus rubra.* Error bars are standard errors.

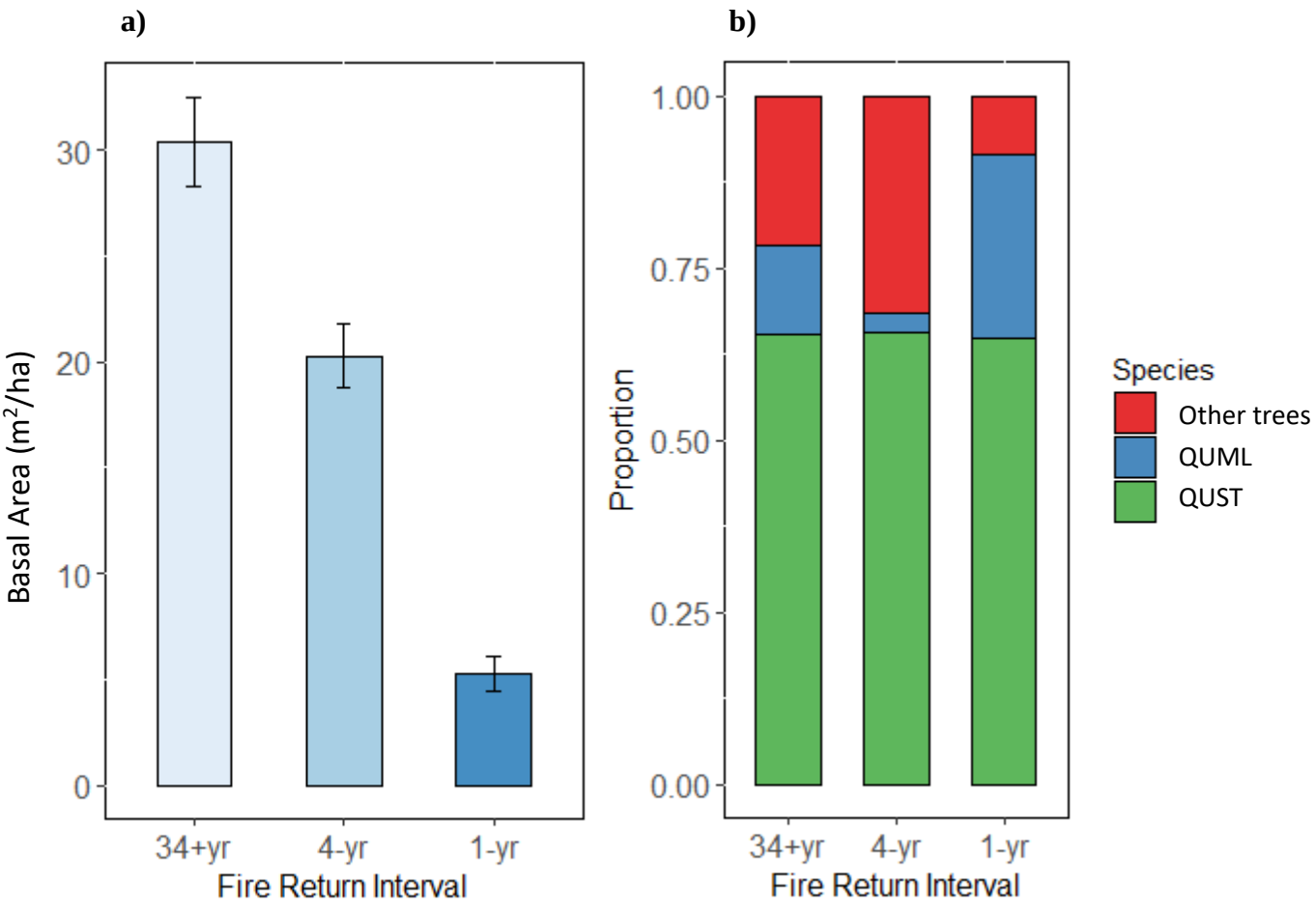


**Figure 4. a)** Mean basal area of selected units at PWMA and **b)** the species composition of selected units at PWMA including *Quercus marilandica* (QUML), *Quercus stellata* (QUST), and other trees, which included *Carya tormentosa*, *Carya texana, Juniperus virginiana*, *Pinus echinata*, *Quercus alba, Quercus velutina*, and *Ulmus alata.* Error bars are standard errors.

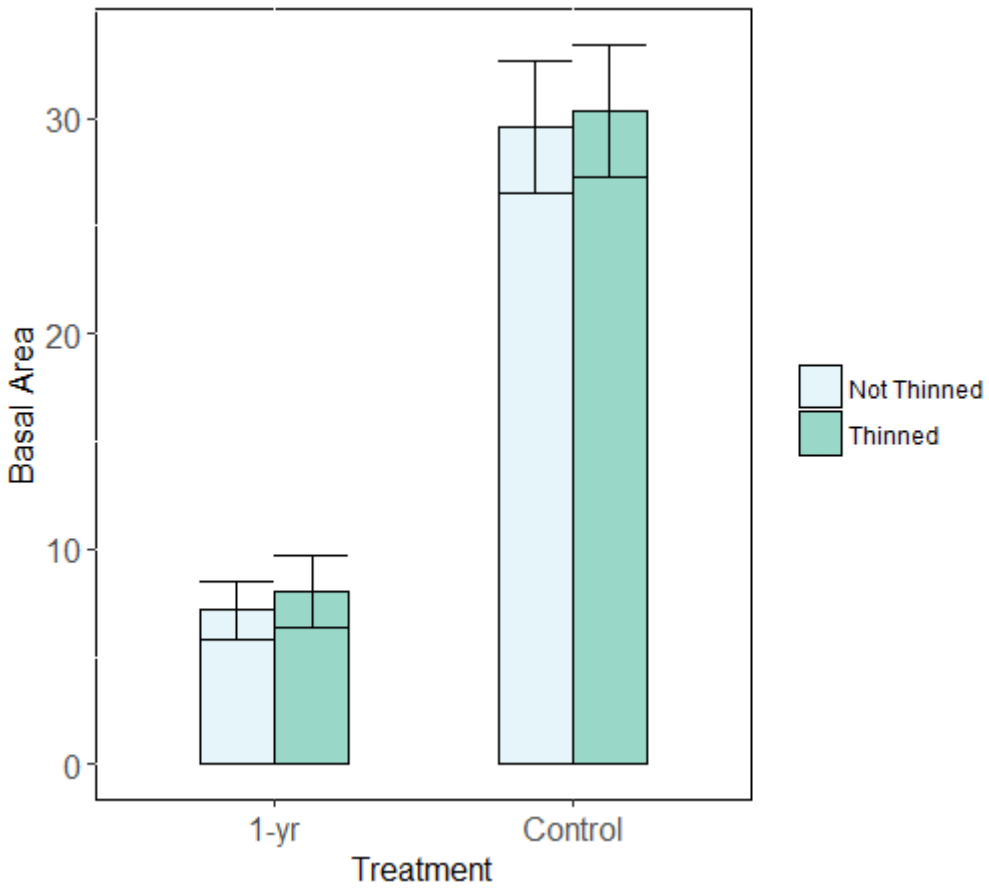


**Figure 5.** Comparison of the basal area of thinned and unthinned treatments with the same fire regime. Thinning was applied by stem-injection in 1984. No differences were found between thinned and unthinned plots experiencing the same fire regime ($p>0.96$). Confidence intervals are vertical lines.

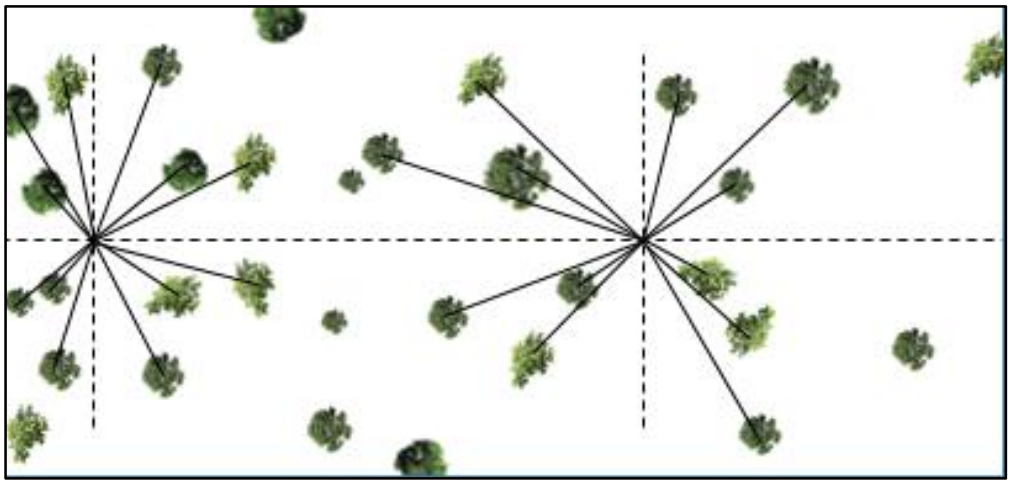

**Fig 6.** Map of a hypothetical forest illustrating the application of the point-centered quarter plot method. The vertical dotted line represents the transect. At the center of the plot, units were divided into four quarters and the nearest three trees were measured as indicated by the solid lines.

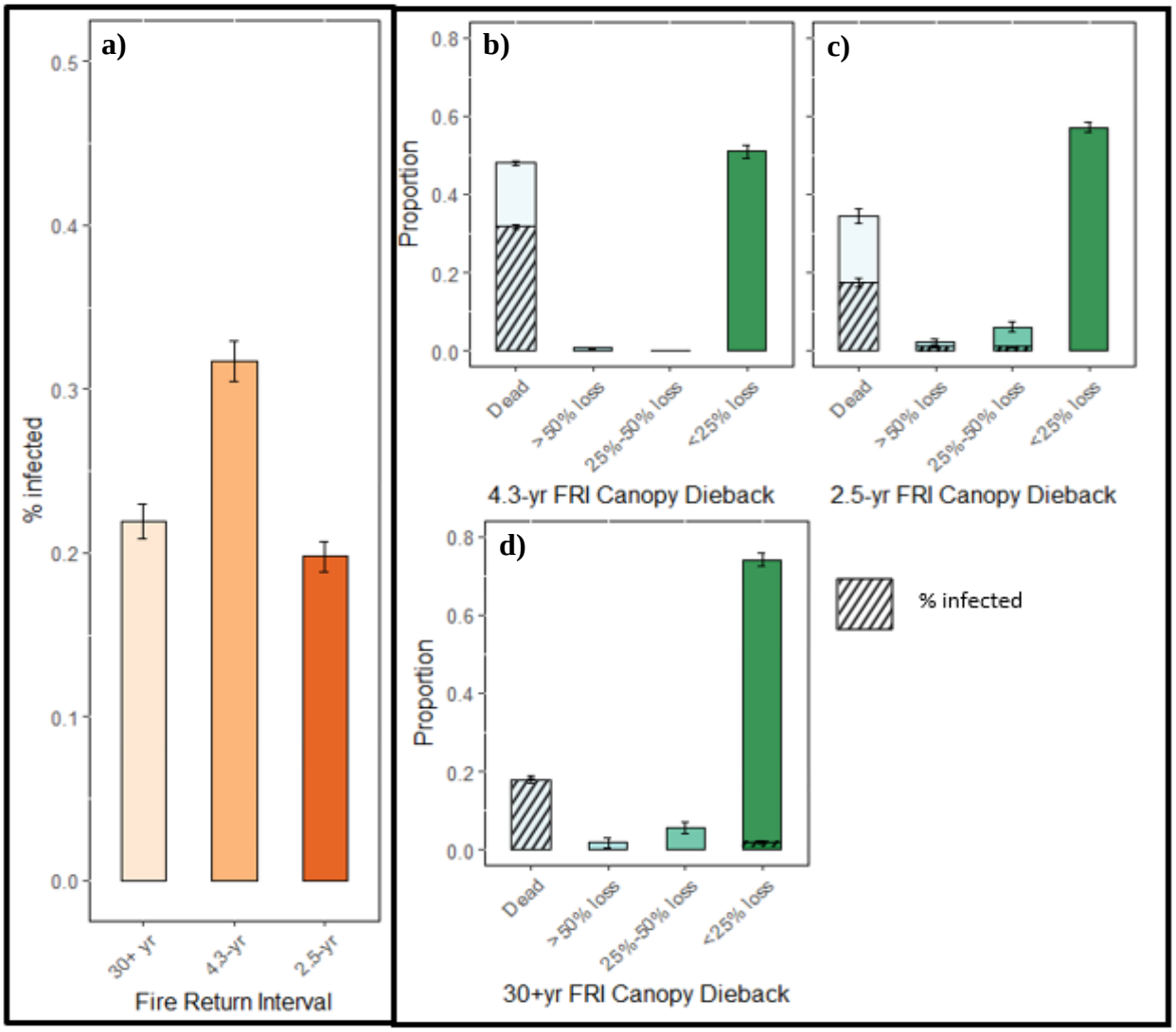


**Fig 7. a)** Percent infection of *Biscogniauxia* spp. at OWMA on total *Quercus* species, based on fire return interval alone ($P$>0.05). The proportion of trees based on canopy dieback (dead, >50% loss of canopy, 25%-50% loss of canopy, <25% loss of canopy)—and the percent that are infected—are represented by **b)** units experiencing 4.3-yr FRI, **c)** units experiencing 2.5-yr FRI, and **d)** units experiencing 30+yr FRI. Both the 4.3-yr FRI (b) and 2.5-yr FRI (c) are less likely to develop *Biscogniauxia* ($P$<0.001) due to the additive effect of canopy dieback and FRI. Vertical error bars are standard errors.

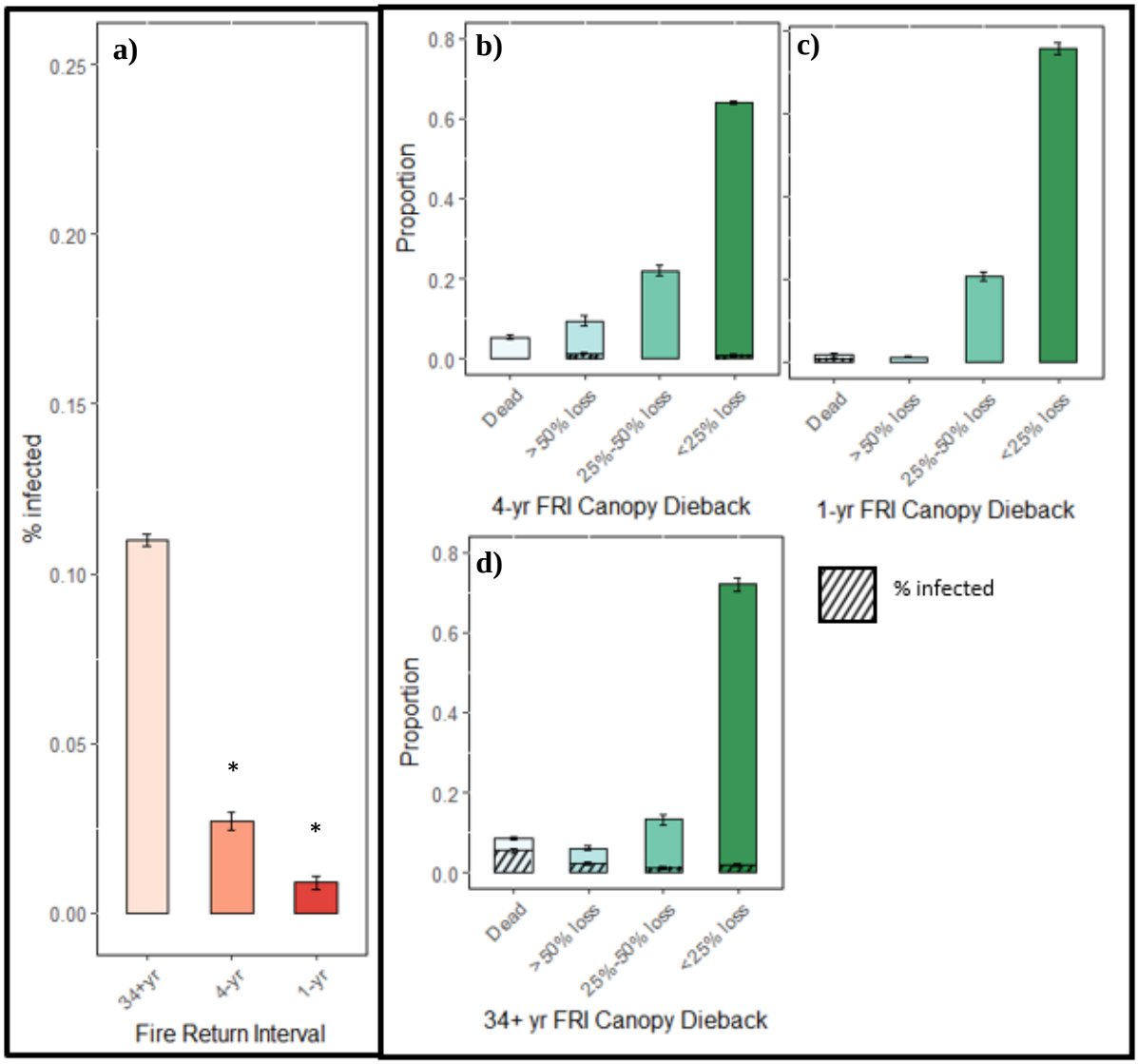


**Fig 8. a)** Percent infection of *Biscogniauxia* spp. at PWMA on total *Quercus* species, based on fire return interval alone ($P<0.05$). Astericks indicate significant differences from the control (34+yr FRI). The proportion of trees based on canopy dieback (dead, >50% loss of canopy, 25%-50% loss of canopy, <25% loss of canopy)—and the percent that are infected—are represented by **b)** units experiencing 4-yr FRI, **c)** units experiencing 1-yr FRI, and **d)** units experiencing 34+yr FRI. Both the 4-yr FRI (b) and 1-yr FRI (c) are less likely to develop *Biscogniauxia* ($P<0.001$). Vertical error bars are standard errors.

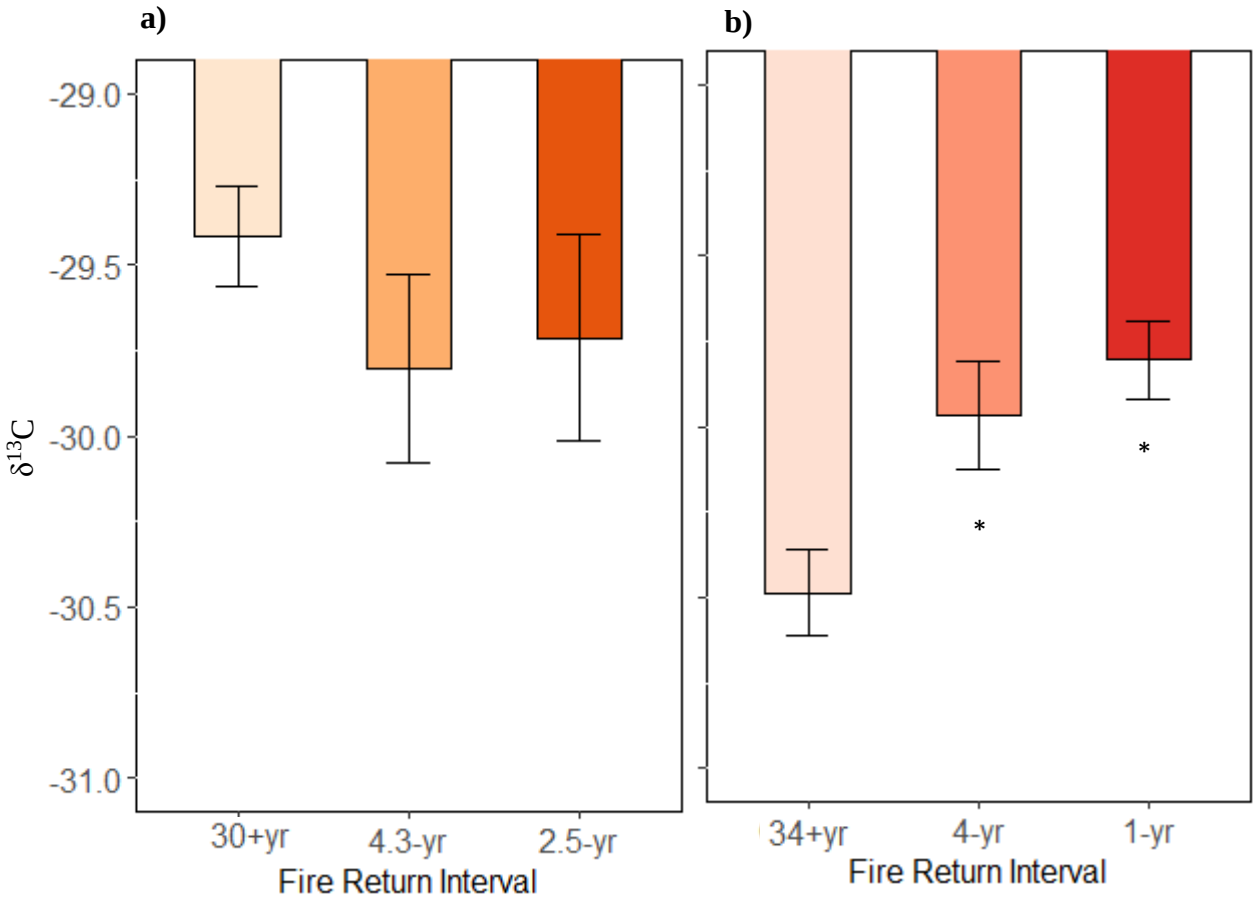


**Figure 9**. Mean leaf $\delta^{13}C$ across treatments at **(a)** Okmulgee Wildlife Management Area (OWMA) and **(b)** Pushmataha Wildlife Management Area (PWMA). **(a)** Differences in $\delta^{13}C$ for were not significant across treatments ($P$>0.40). (**b)** Differences in $\delta^{13}C$ were significant across treatments ($P$ <0.001). Asterisks indicate significant differences from the control treatment (34+yr FRI). Error bars are standard errors.

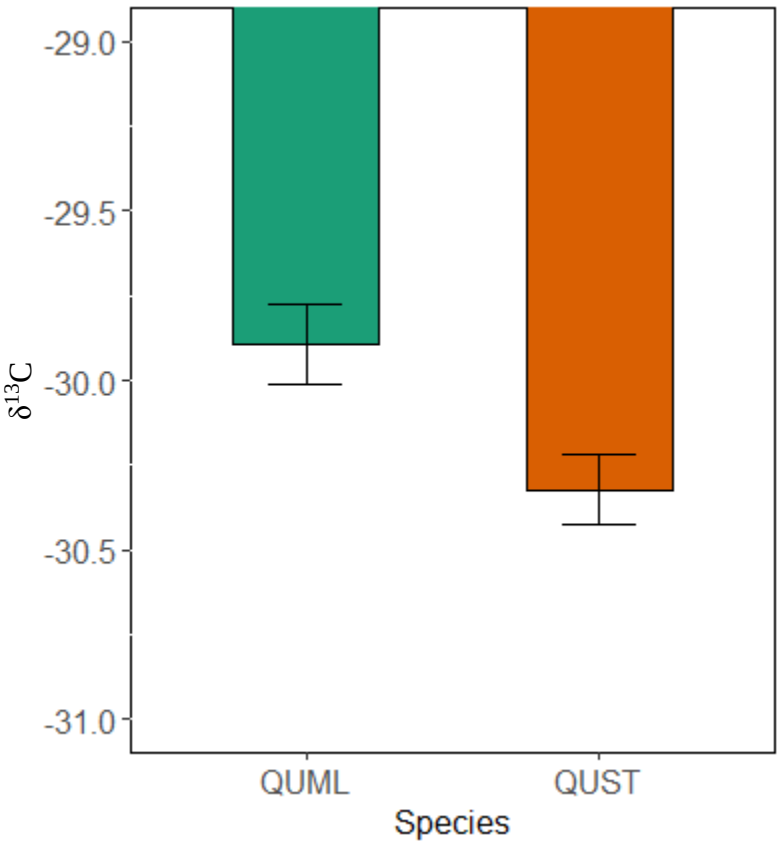


**Fig 10.** Mean leaf $\delta^{13}C$ at Pushmataha Wildlife Management Area (PWMA) for both *Quercus stellata* (QUST) and *Quercus marilandica* (QUML). Differences in $\delta^{13}C$ were significant ($P$ <0.004) between species. Error bars are standard errors.

VITA

Alissa Freeman

Candidate for the Degree of

Master of Science

Thesis: MANAGING BISCOGNIAUXIA PREVALENCE WITH PRESCRIBED FIRE IN OAK DOMINATED FORESTS

Major Field: Botany

Biographical:

Education:

Completed the requirements for the Master of Science in Botany at Oklahoma State University, Stillwater, Oklahoma in July, 2018.

Completed the requirements for the Bachelor of Science in Organismal Biology at University of Kansas, Lawrence, Kansas in 2013.

Experience:

Teaching Assistant in Oklahoma State University from 2016-2018 for General Ecology.

Professional Memberships:

GPSGA Representative in Oklahoma State University from 2016-2017
BGSO President from 2017-2018
Science Club Outreach Coordinator from 2016-2018